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Comparing Observations of Age at First Reproduction in Western Gray Whales to Estimates of Age at Sexual Maturity in Eastern Gray Whales

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ABSTRACT

Age at first reproduction (AFR) is a basic component of age-structured whale assessment models, but direct estimates of this parameter do not exist for either the abundant eastern or critically endangered western population of gray whales (*Eschrichtius robustus*). Instead, assessments of both populations have utilized either of two recognized estimates of eastern gray whale age at sexual maturity (ASM) that are adjusted by a year to account for fetal gestation. These ASM estimates are: 1) 9 years median, 6-12 years range, and 2) 6 years median, 5-9 years range, but there are biases and discrepancies associated with these estimates. Over a decade of individual monitoring of western gray whales on their primary feeding ground off the northeastern coast of Sakhalin Island, Russia, has identified 17 female whales first sighted as calves or yearlings that were potentially sexually mature by the 2009 field season, ranging in age from 5 to 11 years. However, only two of these whales have been observed to have produced a calf, establishing the first observed values of western gray whale AFR as seven and 11 years. While limiting, that only two AFR observations were made is also informative, suggesting that until more information is available, the first eastern gray whale ASM estimate is the more appropriate to use in western gray whale assessments. Overall, eastern and western gray whale assessments would benefit from a concerted effort to collect AFR observations from each population.

KEYWORDS: AGE AT SEXUAL MATURITY; GRAY WHALE; MONITORING; PACIFIC OCEAN; PARTURITION; PHOTO-ID

INTRODUCTION

Age at first reproduction (AFR), also referred to as age at first birth and age at first parturition in studies of mammalian demography, is an important life history descriptor and a necessary parameter in age-structured assessment models of whale populations. In large mammal population dynamics, AFR demonstrates low elasticity, meaning that changes in AFR have less of an effect on the growth rate of a population relative to changes in other population parameters such as adult fecundity and survival (Gaillard *et al*., 2000). However, AFR is one of the more sensitive population parameters to density dependence and other forms of temporal variation and is therefore considered to serve as a major component of regulation in large mammal populations (Eberhardt, 1977; Fowler, 1984).

Gray whales (*Eschrichtius robustus*) presently exist as two geographically and genetically isolated populations along the eastern and western coasts of the North Pacific. The eastern population migrates from winter breeding grounds off Baja California to summer feeding grounds primarily in the Bering and Chukchi Seas and appears to be equilibrating at a size of approximately 20,000 whales (Laake *et al*., 2009). The western population returns to summer feeding grounds in the Okhotsk Sea from unknown breeding grounds that are suspected to be off the southern coast of China (Wang, 1984; Omura, 1988; Kato and Kasuya, 2002). Western gray whales number less than 150 individuals (Bradford *et al*., 2008b; Cooke *et al*., 2008) and are listed as *Critically Endangered* by the International Union for Conservation of Nature (IUCN, 2010).

Direct estimates of AFR do not exist for either population of gray whales. Instead, assessment models of eastern and western gray whale populations have incorporated one of two available estimates of eastern gray whale age at sexual maturity (ASM) that are offset by a year to account for fetal gestation (e.g., Punt and Butterworth, 2002; Wade, 2002; Cooke *et al*., 2008). These ASM estimates were obtained from whales killed in the Russian aboriginal fishery off the Chukotka Peninsula during the 1980's (Blokhin and Tiupeleyev, 1987), as well as from whales taken off central California from 1959 to 1969 under special scientific permits (Rice and Wolman, 1971). In

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combination, these observations indicate that eastern gray whales reach ASM between the ages of five and 12 years (Rice, 1990; IWC, 1993). However, there are biases associated with these estimates of ASM (Rice, 1990). Additionally, ASM is not a reliable measure of AFR, since maturity in one year does not necessarily mean parturition in the year following (DeMaster 1981; Lockyer, 1984).

Over a decade of research on western gray whales on their primary feeding ground off the northeastern coast of Sakhalin Island, Russia, has recently resulted in the first observations of AFR in this population. The primary objective of the present paper is to report what is currently known about AFR in western gray whales. This information is then placed in the context of the aforementioned estimates of eastern gray whale ASM, thereby warranting a discussion of apparent biases associated with these estimates and of inconsistencies in the reporting and use of these values. Clarification of the existing eastern gray whale ASM estimates and the collection of additional AFR measurements from eastern and western gray whales would benefit assessments of both populations.

METHODS AND RESULTS

Following a pilot effort in 1995, a collaborative Russia-U.S. research program was established in 1997 to conduct individual monitoring of western gray whales using photo-identification and genetic techniques (Weller *et al*., 1999, 2002). This study takes place annually during summer months on the primary feeding ground of western gray whales, which is located off the northeastern coast of Sakhalin Island, Russia. Through 2009, 365 surveys were carried out, leading to the photo-identification of 180 whales, including 141 (78.3%) that have been biopsy sampled for genetic research. The photo-identified whales consist of 82 individuals that were first sighted as calves, 63 (76.8%) of which have been biopsy sampled. Calves are approximately 6-8 months of age when sighted off northeastern Sakhalin Island and are identified by their small body size and, in most cases, a constant and close association with a particular adult female whale (Weller *et al.*, 1999).

Assuming that western gray whales can reach sexual maturity as early as the age of five, which has been accepted for eastern gray whales (IWC, 1993), there are 16 known female whales first sighted as calves that were potentially sexually mature by the 2009 field season (i.e., these whales were calves in 2004 or earlier) (Table 1). Additionally, a female whale first observed as a yearling in 2001 (whale G in Table 1), inferred to be a calf in 2000, was also considered to be sexually mature by 2009. A yearling is a whale of approximately 1.5 years of age that was identified as such based on its intermediate size relative to calves and juveniles (Sumich, 1986; Sumich and Harvey, 1986; Perryman *et al*., 2002b) and on the presence of a full year of barnacle (*Cryptolepas rhachianecti*) growth and associated scarring, which produces a clear visual distinction between calves and yearlings in the photographic record. No other females were first identified as yearlings during the study. In 2007, whale G was sighted accompanying a calf, a relationship subsequently confirmed through genetic analysis. In 2009, a whale first observed as a calf in 1998 (whale A in Table 1) was sighted with a calf on multiple occasions, although a biopsy sample of the calf was not obtained. These observations indicate that whale G and whale A produced their first calves at the age of seven and 11 years, respectively.

DISCUSSION

Given the small size of the western gray whale population, relatively few calves are produced each year, providing minimal opportunities to make observations of AFR, even over a long period of monitoring. In this case, after more than a decade of study, only 17 females first identified as calves or yearlings were possibly sexually mature by 2009 (Table 1). There were seven additional whales of unknown sex first identified as calves before or during the 2004 field season (all other 30 calves documented through 2004 are male), but only one of these whales was sighted outside of its birth year and has not been seen since it was approximately 2.5 years of age. Despite the small sample of potentially newly mature females, that only two of them were ultimately observed with a calf is of interest. Several explanations are plausible, beginning with the possibility that the remaining whales were not yet sexually mature. While it is reported that some eastern gray whales attain sexual maturity as early as the age of five (IWC, 1993), others mature later, including ages exceeding those of the western gray whales in Table 1 (Rice and Wolman, 1971). Further, some of these young females may have reached sexual maturity by 2009, but perhaps they failed to conceive by or were pregnant in that year. Alternatively, one or more of these whales may have given birth prior to the 2009 field season, but the calf was lost before the season or undetected on the feeding ground. Finally, it is possible that not all of these females are presently alive, as six of them have not been observed in years subsequent to being identified as a calf, and four others have not been sighted in three or more years.

Table 1

Annual records of potentially sexually mature female western gray whales first sighted as calves or yearlings (n=17) off northeastern Sakhalin Island, Russia through 2009. Note that no females were first sighted as calves or yearlings prior to 1998. C=photographically identified as a calf, Y=photographically identified as a yearling, M=photographically identified with a calf, and 1=photographically identified.

Whale	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
A	C	1	1	1	1	1	1	1	1		1	M
B	C	1	1									
C				C	1	1	1	1	1			1
D				C								
E				C	1	1	1				1	1
F				C	1	1	1					
G				Y	1	1	1	1	1	M		1
H					C	1	1	1	1			
I					C	1	1					
J					C							
K						C						
L						C						
M						C				1		
N							C	1	1	1	1	
O							C					
P							C					
Q							C	1		1		

The newly matured whales that were detected with a calf establish the first observations of western gray whale AFR as seven and 11 years. While limited inference can be made from only two observations, some factors are of note. For whale G to have produced a calf at the age of seven, she became sexually mature no later than age six, which is within the range and toward the lower bound of both ASM estimates for eastern gray whales (Rice and Wolman, 1971; Blokhin and Tiupeleyev, 1987; IWC, 1993). Unless western gray whales are physically capable of maturing earlier than eastern gray whales (a suggestion not supported by the findings in Table 1), it is unlikely that whale G produced a calf before 2007, as such timing would be suggestive of an ASM of four years or less, given the minimum two-year calving interval documented for eastern and western gray whales (Jones, 1990; Bradford *et al*., 2008b). Regarding whale A, she became sexually mature no later than age 10, in order to have produced a calf at age 11, which is within the range of one of the eastern gray whale ASM estimates (Rice and Wolman, 1971; IWC, 1993; see below). There is a possibility that whale A produced a calf prior to 2009, but either lost it or it was undetected on the feeding ground. However, the pronounced site fidelity of whale A (Table 1) and the fact that, while uncommon, calves can be first identified after weaning has occurred, challenges the latter suggestion. Of the six calves first sighted post-weaning between 2003 and 2007 (i.e., the time period when whale A potentially reached sexual maturity and could have produced a previous calf), four have been biopsy sampled and can be excluded as possible offspring of whale A.

Compensatory density-dependent mechanisms predict a maximized reproductive output from the depleted western gray whale population, including a lowered AFR (Fowler, 1984). However, the information summarized in Table 1, while limited, indicates that a minimization of AFR in western gray whales is not occurring, although magnified demographic stochasticity is also expected at small population sizes (Lande, 1993). Further, environmental variability and its impact on the nutritional status of reproductive females may be regulating calf production in western gray whales (Brownell and Weller, 2002; Bradford *et al.* 2008a), as has been suggested for eastern gray whales (Perryman *et al*., 2002a). Clearly, more observations are needed to attempt a meaningful interpretation of the factors affecting AFR in western gray whales.

The AFR observations presented here do not challenge the continued use of eastern gray whale ASM estimates in population assessments of western gray whales. However, a discussion of biases associated with these estimates is needed, as is an overview of the inconsistent treatment of these estimates in the published literature. The IWC (1993) recognizes two estimates of eastern gray whale ASM: 1) 9 years median, 6-12 years range, and 2) 6 years median, 5-9 years range, citing the unpublished paper of Rice (1990) as the summary source of these published estimates. Rice (1990) explains that the first ASM estimate is a corrected version of that determined by Rice and Wolman (1971), accounting for the underestimation of whale ages by one year in the original study. Initially it was assumed that gray whales deposit two ear plug growth layers (used for age determination) in the first year of life and then one layer thereafter (Rice and Wolman, 1971), but recent evidence indicates that one growth layer accumulates annually throughout the life of the whale (Blokhin and Tiupeleyev, 1987; Rice, 1990). In their study, Rice and Wolman (1971) considered any female whale that had attained puberty (i.e., had a corpus luteum or at least one corpus albicans in the ovaries) as an adult and then examined the percentage of adult whales relative to the number of ear plug growth layers, plotting the results for both males and females. Using a running mean to combine values from both sexes, Rice and Wolman (1971) found that 50% of whales were mature at nine growth layers. For males and females, they also report that the fewest growth layers found in an adult whale was six and that the highest number in an immature whale was 11, aside from one female with 13. Thus, they conclude that ASM for both sexes ranges from “[six] to at least [12] years” (using corrected ages). Given that female ASM is the relevant component in terms of population assessments, it is unclear why subsequent use of this range has fixed the upper bound as 12, when it is possible that not all females are mature by this age. Rice and Wolman (1971) also point out that their ASM estimate might not be completely reliable due to a notable difficulty in counting ear plug growth layers from immature whales.

Rice (1990) attributes the second estimate of ASM to Blokhin and Tiupeleyev (1987), although he reports the female estimate as 7 years median, range 5-8, which differs from the summary in IWC (1993). To determine their estimate of ASM, Blokhin and Tiupeleyev (1987) regressed the number of corpora albicantia against the number of ear plug growth layers. They do not mention how sampled whales with a corpus luteum, presumably mature (Rice and Wolman, 1971), were considered in the analysis. Blokhin and Tiupeleyev (1987) found that 50% of females in their sample were mature by seven years of age and that all females were mature by eight years. A lower bound of five years is not mentioned in the paper, and the regression plot indicates that none of the sampled whales with five growth layers had corpora albicantia. Perhaps a subsequent analysis or interpretation of the raw or summary data of Blokhin and Tiupeleyev (1987) resulted in establishing a lower bound for the ASM estimate (Rice, 1990) and eventually decreasing the median and elevating the upper bound (IWC, 1993), but an associated explanation was not located. Thus, the basis of the ASM distribution of 5-9 years utilized in recent assessments of both eastern (Punt and Butterworth, 2002; Wade, 2002) and western (Bradford *et al.* 2008b) gray whales cannot be fully resolved.

Techniques for estimating the average ASM in marine mammals are reviewed in DeMaster (1984). The approach used by Rice and Wolman (1971) to determine ASM is equivalent to estimator no. 3 in DeMaster (1984), and the method of Blokhin and Tiupeleyev (1987) is similar to estimator no. 4, although neither analysis was oriented toward estimating an average ASM *per se*. As the average mean age at first ovulation is considered the only unbiased estimate of ASM, there are biases associated with both of these techniques and the results may not be directly comparable (DeMaster, 1984). Given the greater representation by parous females in the two studies, it seems plausible that both analyses overestimate ASM in eastern gray whales. Rice and Wolman (1971) pointed out that five of the 15 nulliparous and primiparous females in their sample had one or more corpora albicantia (considered to be derived from corpora lutea of ovulation), in addition to a corpus luteum, meaning that these whales had reached puberty but had not conceived in the year before they last went into estrus. While adding the gestation period to an unbiased measurement of ASM may underestimate AFR (DeMaster, 1981), the relationship between the existing eastern gray whale ASM estimates, gestation, and AFR is not readily apparent. One final consideration regarding the estimates of eastern gray whale ASM is that only half of the sampled individuals could be aged in the associated studies, with the remaining individuals having unreadable ear plugs (Rice and Wolman, 1971; Blokhin and Tiupeleyev, 1987). Presumably, whales with readable ear plugs are representative of the greater sample in terms of reproductive parameters, although this has not been explicitly addressed. Regardless, even in readable ear plugs, growth layers are not always well-defined, particularly in immature whales (Rice and Wolman, 1971). Thus, imprecise aging may be an additional source of bias in the estimates of eastern gray whale ASM.

The available estimates of eastern gray whale ASM are in need of clarification and reanalysis, such as that initiated by Brandon *et al.* (2005). However, unavoidable biases will remain and the connection between ASM and AFR in gray whales will continue to be undefined. Using biased and imprecise estimates of ASM as a basis for AFR in gray whale population models has likely not led to substantial biases in assessment results, given the low elasticity of AFR, but it limits opportunities to make inference about a parameter that is particularly responsive to temporal variation (Gaillard *et al.*, 2000). While estimates of gray whale AFR would also be subject to bias, they would provide a more direct measure of recruitment as needed for assessment, and emphasis should be placed on determining AFR in both populations. Aside from the western gray whale AFR observations presented here, only one other observation is known for the species. In 1983, researchers in Laguna San Ignacio, Baja California, Mexico, observed a calf accompanying a female eastern gray whale that had been sighted annually since first being identified as a yearling in 1977, indicating that she had first given birth at the age of seven years (S.L. Swartz, pers.

comm.). Results of the Russia-U.S. research program suggest that until more AFR observations are obtained, incorporating ASM as determined by Rice and Wolman (1971) into future western gray whale assessments would be a more conservative approach for this critically endangered population.

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